THE ORIGIN OF THE MAMMALIAN CARPUS AND TARSUS.

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(Plate VII.)

Few problems in biology are of greater interest than that of the origin of mammals, and within the last thirty years much discussion has been given to the problem. The majority of embryologists, from the consideration of certain developmental conditions, have been led to the conclusion that the mammals have been descended from some Batrachian ancestor or some even more primitive form which may have lived in Devonian times. Most palæontologists, on the other hand, have considered that in the Theriodont and Dicynodont reptiles we have forms which are so strikingly mammal-like that the ancestral mammal should be looked for either in one of these groups or in some closely allied order. As recent investigations point pretty conclusively to the fact of the mammalian skull being directly descended from that of the Theriodont, it becomes important to see if the evidence derived from other parts of the skeleton confirms that given by the skull. Already the shoulder girdle of the Anomodont has been shown to be essentially similar to that of the Monotreme (1), while that of the Monotreme resembles closely that of the fœtal Marsupial (2). In the present paper I hope to show that the evidence derived from the study of the carpus and tarsus confirms that of the skull and shoulder girdle. Unfortunately the carpi and tarsi of the fossil reptiles are much less perfectly known than most other parts of the skeleton, since unless the various elements are found in undisturbed position the evidence derived from them is not of a very satisfactory nature. Still it is possible even at present to show from the few well-preserved specimens known that the mammals must have been derived from some Synapsidan reptile.

In the Stegocephalia the carpus is usually but imperfectly ossified. In Eryops, however, it is well ossified, and fortunately a well-preserved specimen is known (3). As preserved there are four bones in the proximal row, five in the distal, and two other elements in the centre. By Cope the four proximal bones are believed to be Radiale, Centrale, Intermedium, and Ulnare. By Emery (4) they are looked upon as the Radiale, Paracentrale, Intermedium, and Ulnare. While it is difficult for one who has only the figures to go by to give a very decided opinion, I should like to suggest that the four proximal elements are probably homologous with the four proximal elements found in the carpi of most primitive reptiles and well seen in Sphenodon, viz., Radiale, Intermedium, Ulnare, and Pisiform. The two central elements are undoubtedly centralia 1 and 2, while the five distal elements are as certainly carpalia 1–5. The carpus of Eryops would thus seem to agree closely with that of Sphenodon, and no doubt represents a slight specialisation of the primitive form from which the carpi of all the higher animals have been derived.

It is probable that in early Permian or late Carboniferous times some member of the Stegocephalia gave rise to the Cotylosauria. This order, though of the greatest interest as containing most probably the ancestors of all the later reptiles, both of the Synapsidan and Diapsidan groups, is at present only imperfectly known. An imperfect carpus of Pariotichus has been described (5), but as the elements were not found in position it is difficult to place much reliance on it. The carpus in Pareiasaurus has not been described, but Huene (6) has recently figured the fairly well-preserved carpus of the allied genus Sclerosaurus. In his Taf. I. he indicates four elements as carpalia 1–4, and this identification seems probably correct. Proximal to C 3 and C 4, and situated immediately distal to the Ulna, is another element, almost certainly the Ulnare. In Taf. II. what is evidently the counterpart of this Ulnare is marked "Pisiform," and a more proximal bone is marked "Ulnare." What is regarded as Ulnare in Taf. II. seems to me to be a portion of the Ulna. The element between the Radius and Ulna, and which Huene regards as the Radiale, I should incline to regard as the Intermedium. The element marked C 3 in Taf. II. does not appear to be the same as C 3 in Taf. I., and is in my opinion the centrale. It is thus probable that the Cotylosaurian carpus consisted of four proximal elements, a centrale, and four distal elements. While the specimen of Sclerosaurus practically proves these elements to have been present, it does not disprove the presence of a second centrale, and as many of the descendants of the Cotylosaurus retain two

centralia, we may conclude that two centralia existed in the Cotylosaurian carpus.

In Procolophon (7, 8, 9), the Diaptosaurian, most nearly related to the Cotylosaurs, the carpus is fortunately well known. Proximally there are a well-developed pisiform, a large ulnare, and a fair-sized narrow intermedium. The radiale appears to have been cartilaginous. In the centre of the carpus are two centralia, and distally there are four carpalia. If the radiale is rightly regarded as having been cartilaginous, then the carpus would appear to have agreed with that of Eryops as regards the elements except that in Procolophon the carpale 5 is absent or cartilaginous.

The structure of the skull renders it probable that the Therocephalians are the direct descendants of the Cotylosaurs in the line which gave rise to the Mammalia. Of the Therocephalians the only carpus known is that of Theriodesmus (10). Fortunately the specimen is well preserved and the degree of displacement of the bones so slight that there can be little doubt as to the interpretation of the various elements. Bardeleben (11) has recently redescribed and figured the carpus. He has shown that there are four bones in the proximal row—radiale, intermedium, ulnare, and pisiform—two centralia and four carpalia. The figure of the carpus which I give is only a slight modification of that given by Bardeleben.

Among the Dicynodonts the carpus is pretty well known. In most genera it is well ossified, but in the aquatic Lystrosaurus it is mainly cartilaginous. The only Endothiodont carpus known is that of *Opisthoctenodon agilis*, but fortunately this is known by a fairly satisfactory specimen. As in most primitive reptiles, the proximal row consists of four bones—a broad short radiale, a small intermedium, a large ulnare, and a rather small pisiform. In the centre of the carpus are two broad centralia. The distal row is formed of a large carpale 1, small carpalia 2 and 3, and a large carpale 4. On the radial side of the carpus as preserved are three small bones, which may belong to the hand, but as the specimen is of very small size and crushed in on the base of the skull, it is impossible to be quite certain of the nature of the fragments. I have figured them as they occur. The two bones adjoining the first carpale and first metacarpal are probably the bones of a prepollex, as in Theriodesmus. The third little bone possibly does not belong to the manus.

The carpus of Oudenodon (12) I have already elsewhere described. It closely resembles that of Opisthoctenodon, but there appears to be no trace of a prepollex. The proximal row consists of radiale, intermedium, ulnare, and pisiform. There are two centralia, and apparently five carpalia. It is doubtful if the fifth carpale is really

distinct from the fourth, but there is some evidence of its having been distinct. In my previous description of this carpus I mistook the first carpale for the first metacarpal.

It is unfortunate that in the Theriodontia the group from which the mammals appear to have directly sprung, only one carpus is at present known, and that an imperfect one. This is the carpus of *Microgomphodon eumerus* (13) described and figured by Seeley. Seeley considers there are three bones in the proximal row, but as it is very probable that the large element with which the ulna articulates is not the pisiform as Seeley believes, but the ulnare, and that the pisiform is missing, it seems likely that the proximal row in the Theriodonts has four bones, as in the more primitive groups and the majority of mammals. There appears to be only one centrale, and only four carpalia. It is possible, however, that the element between the radiale and the ulnare is not the intermedium, but a second centrale, and that the intermedium is not seen in the specimen. The arrangement of the bones in the Endothiodont carpus suggests this possibility. It is impossible to decide the point by the figure.

The examination of the series of carpi shows that there has been very little evolution in the carpus from the higher Labyrinthodonts to the Theriodonts. The fifth carpale becomes lost, but otherwise any of the carpi from the Cotylosaurians to the Theriodonts might be the one from which the mammalian type has been derived.

The stages in the evolution of the tarsus, though they are less fully known than the stages of the carpus, throw much more light on the line of descent of the mammals.

The Labyrinthodont tarsus is practically unknown. The tarsus of the primitive Stegocephalian Archegosaurus is known, but there is some difference of opinion as to its interpretation. Its most interesting feature is that it consists of at least nine distinct elements, and certain of these may represent the fusion of two. But while the Stegocephalian tarsus contains so many distinct elements, the number is found to be very considerably reduced in all the descendants. In some the reduction appears to be due to a number of the elements uniting together; in others the reduction is evidently due to some of the original elements being lost.

In the Cotylosauria the tarsus is very imperfectly known. In Pareiasaurus and Sclerosaurus there is a large tarsal bone probably made up of the united tibiale, intermedium, and fibulare. The other elements have possibly been cartilaginous. Case has figured a fairly satisfactory tarsus of Pariotichus (5). It shows that the proximal tarsal row consists of two distinct bones—either tibiale and fibulare, or with possibly an intermedium united to one of the other

two elements. There are probably five tarsalia and a distinct centrale.

In Procolophon (7) the tarsus consists of six bones, but the intermedium is manifestly united with the tibiale, and it is not improbable that the centrale is united with the fibulare. There are only four tarsalia ossified. In other primitive Diaptosaurians five tarsalia are ossified.

In Sphenodon (14) the structure and development of the tarsus have been very fully worked out by Howes and Swinnerton; and though Sphenodon has advanced far from the point of separation of the Diapsida and the Synapsida, it gives us perhaps a better idea of the primitive type of the Reptilian tarsus than we get from most of the fossil specimens. Here we find that the tarsus in its early development consists of a moderate-sized fibulare and tibiale, a large intermedium, a rather small centrale, and four tarsalia.

Unfortunately no Therocephalian tarsus is known, so that the intermediate stages between the Cotylosaurian types and the Dicynodont are at present hypothetical.

The Dicynodont type is fortunately now fully known. A few years ago I described the tarsus of Oudenodon (12), and since then have had the opportunity of examining two other Dicynodont tarsi. The tarsus of *Oudenodon trigoniceps* has been somewhat more fully developed, and a slight modification is required of my previous description. The small element which I regarded as the centrale has been found to be really a part of the tibial. The intermedium, however, seems to be a distinct element. The first row of the tarsus thus consists of a large semicircular tibiale, and a somewhat larger fibulare, with a small intermedium fitted in between them. The distal row is formed of four bones, of which the first is large and almost like a metatarsal. Between the tibiale and the first tarsale there is a moderate-sized gap in which it is moderately certain there was a cartilaginous centrale. The second Dicynodont tarsus I have examined probably also belongs to a species of Oudenodon, and while it agrees closely with that of *O. trigoniceps* it shows a distinct ossified centrale between the tibiale and first tarsale. The centrale is not fully ossified like the other elements, but has the appearance of an imperfectly ossified cartilaginous element. The third tarsus is a specimen in the Albany Museum—probably belonging to a species of Dicynodon. Here the most noteworthy feature is the presence of a large fully ossified centrale, which articulates with the tibiale and with probably all four tarsalia. The Dicynodont tarsus, with the exception of having a distinct intermedium, is thus seen to be practically of the mammalian type.

Only one Theriodont tarsus is known—that of Microgomphodon (13)—and unfortunately it is not satisfactorily preserved. It agrees, however, with the Dicynodont tarsus in having the tibiale and fibulare of large size. According to Seeley the calcaneum (=fibulare) "does not develop a posterior heel process." As, however, only the anterior or upper surface of the tarsus seems to be displayed, it is difficult to see what evidence there is for this statement. In the Dicynodont fibulare there is a distinct heel process, and it is highly probable that one also exists in the Theriodonts. There is in the tarsus of Microgomphodon a wide space between the tibiale and the first tarsale, so that the condition of the Theriodont tarsus is probably very similar to that in the Dicynodont, there being evidently either a cartilaginous centrale or a bony centrale which is lost from the specimen.

While the mammalian carpus has become very slightly specialised, and is hence of little service in guiding us to the mammalian ancestor, the specialisation of the tarsus is so peculiar that all claimants to the honour of being the immediate forefathers of the mammals may be dismissed if they do not show some approximation to a similar specialisation. We may thus put on one side all modern types of reptiles and all the Amphibia, none of which can have any claim to be the immediate mammalian ancestor, and we have left the Cotylosaurians, some of the primitive Diaptosaurians, the Therocephalians, and the Dicynodonts and Theriodonts. In these latter we find more or less approximation to the mammalian type, but if we take into consideration the extreme mammalian specialisation—the presence of a large tibiale and fibulare with a centrale which is not in the centre but comes between the tibiale and the first tarsale—then we are driven to the conclusion that the mammalian ancestor must have been a Dicynodont, a Theriodont, or a form belonging to a closely allied order. From the examination of the skull we have good reason to believe that the ancestor was a Theriodont, and the evidence of the tarsus fully confirms that derived from the skull and other parts of the skeleton, and the carpus, while it does not add any very strong evidence, certainly does not afford any evidence that is not also in harmony with this conclusion.

Addendum (Oct. 20, 1904):—Case has recently published a short paper "On the Structure of the Fore Foot of Dimetrodon" (Journ. Geol., vol. xii., No. 4, May–June, 1904), in which he figures an almost perfect carpus, and shows that it is strikingly like the carpus of Procolophon. The only differences of importance are that in Dimetrodon the radiale is large and fully ossified, and that there is a distinct ossified fifth carpale.—R.B.

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(14) Howes and Swinnerton. "On the Development of the Skeleton of the Tuatara, &c.," Tr. Zool. Soc., 1901.

REFERENCES TO PLATE.

Fig.

1. Carpus of Eryops. After Emery. Slightly modified. Reduced.
2. Carpus of Sphenodon, juv. After Howes and Swinnerton. Enlarged.
3. Carpus of Procolophon. Slightly enlarged.
4. Carpus of Theriodesmus. Arrangement restored.
5. Carpus of *Opisthoctenodon agilis*. Enlarged.
6. Carpus of *Oudenodon trigoniceps*. Slightly enlarged.
7. Tarsus of Procolophon. Slightly enlarged.
8. Tarsus of *Oudenodon trigoniceps*. Slightly enlarged.